

OBSERVATIONS AND REMARKS ON THE SLAVE-
MAKING RAIDS OF THREE SPECIES OF ANTS
FOUND AT URBANA, ILLINOIS*†

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During the summers of 1925 and 1926, three species of slave-making ants were encountered at Urbana, Illinois, two of which were the facultative slave-makers, *Formica sanguinea* subsp. *subintegra* Emery and *Formica sanguinea* subsp. *rubicunda* Emery, and the third, the true slave-maker, *Polyergus rufescens* subsp. *breviceps* Emery. The two former species are called facultative slave-makers because the ants can subsist without the aid of slaves, that is, their colonies are sometimes slaveless, whereas *Polyergus rufescens* subsp. *breviceps* Emery is entirely dependent on its slaves for food, the rearing of its young and the construction of its nests.

Most of the notes presented here deal with the raids and habits of *Formica sanguinea* subsp. *subintegra* Emery. A colony of this species was very accessible for study, since it was located on the lawn in front of the Natural History Building of the University of Illinois and not over seventy-five yards from the writer's office.

Formica sanguinea subsp. *subintegra* Emery

This ant is perhaps the most common of our eastern *sanguineas*. It occurs at low elevations throughout the area from Canada to Georgia, and westward to the Dakotas and Kansas. The workers can be readily distinguished from their nearest relatives by their distinctly brown-colored gasters and their thick, blunt petioles.

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The workers also have rounder heads and smaller bodies than the other species of *sanguinea*.

In the vicinity of Urbana, the common slave of *subintegra* is the black, field or lawn ant, *Formica fusca* var. *subsericea* Say, one of our most common ants not only at Urbana but throughout most of the United States. Wheeler (1913) records the following species of ants as slaves of *subintegra*: *Formica fusca* var. *subaenescens* Emery, *F. cinerea* var. *neccinerea* Wheeler, *F. neogagates* Emery, *F. neogagates lasioides* var. *vetula* Wheeler, *F. pallide fulva schaufussi* Mayr and var. *incerta* Emery, and *Formica pallide fulva nitidiventris* Emery and its variety *fuscata* Emery. It can be seen from this list that *subintegra* makes slaves of a large number of species of ants, all of which belong to the genus *Formica*.

During two consecutive summers, fifteen raids by these ants were witnessed; eleven of which took place in 1925, and the remaining four in 1926. The data relative to these raids are shown in Table I.

TABLE I

Showing details of various raids made by the ants, *Formica sanguinea* subsp. *subintegra* Emery, on colonies of the slave-species, *Formica fusca* var. *subsericea* Say, all raids having taken place from the same colony of the slavemaker.

Month and Day	Hour	Weather Conditions	Distance between Nests	Success of Raid	Time Lasted	
					Hours	Minutes
1925						
July 2	5 P. M.		25 feet	Good		
July 10	12 M.		20 "	Poor		
Aug. 7	4.30 P. M.	Cloudy—muggy				
Aug. 8	1.40 P. M.		70 "	Good	1	40
Aug. 10	3.50 P. M.	Misty—rain	48 "			
Aug. 11	11.55 A. M.	Raining—gently				
Aug. 13	12.10 M.	Clear—warm	98 "	Good	1	20
Aug. 15	4.45 P. M.		150 "			
Aug. 21	11.45 A. M.	Clear—warm				
Aug. 22	4.25 P. M.	Clear—warm				
Aug. 31	11.30 A. M.	Clear—warm	35 "	Good		
1926						
July 8	11 A. M.	Cloudy—cool				
July 13	2.05 P. M.	Clear—cool	38 "	Poor		
July 14	12.15 P. M.	Cloudy—cool	35 "	Good		
July 17	2.05 P. M.	Clear—warm	110 "	Good		

The earliest raid observed took place on July 2, 1925, at which time the *subintegra* workers ransacked a healthy colony of the *subsericea* and drove not only the workers from the nest but also eleven females, ten of which were alate. This is mentioned to support the theory that the raids very probably do not take place until the sexed individuals of the slave-species are mature. If the workers of *subintegra* should raid the nest of the slave-species early enough to obtain the sexed pupæ, these pupæ when carried to the *subintegra* nest would upon obtaining maturity probably endanger the life of the colony of *subintegra*, hence the delay upon the part of the slave-makers in carrying out these raids. Not only have alate females of *subsericea* been found as early as July 2, but also alate females of *subintegra*. Alate females were found in the *subintegra* nest as late as July 13, although at least two raids had previously taken place from this colony.

That *P. subintegra* workers raid the nests of the slave species in their vicinity time and again is proven by the fact that during the summer of 1925, eleven raids were witnessed, and there were probably many others which took place unknown to me. I do not believe that hunger is the sole motive which drives these ants to raid the nests of the slave-species, for the *subintegra* workers raided too often to have exhausted the food supply which they obtained from previous raids.

The conflicts that took place between the two species were indeed mild affairs, which in nearly every case resulted in few deaths on either side. The *subsericea* workers, if time permitted, seized their brood and fled from the nest at the approach of the *subintegra* workers. If sufficiently hard pressed by the raiders, they would even desert their brood and flee to the nearby grass and leaves where they hid while the raiders entered their nest and appropriated any larvæ, pupæ or callows that could be found. The *subintegra* workers when transporting a *subsericea* callow would catch it by the dorsum of the thorax and carry the ant with its ventral surface facing the ground. *Subintegra* workers were even seen to carry some of the *subsericea* callows down into their nests. There is a probability that the *subsericea* callows might reach maturity within the nests of the slave-makers and be accepted by them, especially if the callows were young enough

not to have acquired the *subsericea* nest odor. The custom of carrying callows of the slave species to their nests is a strange habit and one difficult to explain. The only plausible reason that occurs to me is that the workers of *subintegra* are unwilling to return to their nests, empty-handed, so to speak, and hence seize the *subsericea* callows rather than go back to their nests with nothing to show for their efforts.

In several of the raids, the *subsericea* workers offered strong resistance, but this was usually easily overcome by the robust raiders who pounced upon them and not only attempted to pull off their appendages but squirted formic acid on their bodies and wounds. Sometimes as many as three or four *subintegra* workers were observed to attack a single *subsericea* worker.

No one has ever seen the workers of *Polyergus* raid in the morning, but this does not apply for the *subintegra* for they raid at nearly all hours of the day. I have observed raids which took place as early as eleven o'clock in the morning and as late as five o'clock in the afternoon. The majority of these raids, however, occurred between the hours of eleven o'clock in the forenoon and two o'clock in the afternoon, at which time the temperature was probably as high as it is during any part of the day. Wheeler (1916) has noted that *Polyergus* females have made raids with their sister workers, but nothing like this has been observed for *subintegra* or *rubicunda*.

The type of weather is apparently of little importance in determining the raids, for raids have been observed to occur in all types of weather—during misty rains, or on cloudy, muggy days, but most generally on clear, sunny days.

In some of the raids certain *subintegra* workers have been noted to return to their nest with other *subintegra* workers in their mouths. In such cases the transporting ant locked mandibles with the transportee and the latter curled up in such a manner that its ventral side was next to that of the ventral side of the transporter. Why these ants should carry one another is also another perplexing question which has not yet been solved. Whenever I captured a pair acting in this peculiar manner and examined the transported ant, invariably I found it in an apparently healthy condition and as capable of locomotion as the

ant transporting it. This precludes the supposition that the ants were injured, or possibly sick; hence I am led to conclude that the transported ant is either stubborn and refuses to return to its nest or else that the carrying instinct is so well developed in the *sanguinea* worker that rather than return empty-handed she carries home a worker of her own species. I have also observed this act of phoresy for *Formica fusca* var. *argentea* Wheeler, a non-slave making ant. Wheeler has suggested that in the case of the non-slave-making ants such habits may be due to the fact that the transporting ant knows the trail and the transportee does not, or else that the transportee does not wish to change its location and the transporter does.

While the raids of the *subintegra* workers were in progress their slaves usually remained at home with their brood, or else foraged for food in the vicinity of their nest, or in exceptional cases accompanied the slave-makers, though they did not take any active part in the raiding. In only one case have I found a *subsericea* slave-worker returning to the nest of the *subintegra* with a pupa of the raided species in its mouth. This instance was so unusual that it can be considered exceptional. Some writers state that the slaves in the *subintegra* nest show much excitement over the return of the raiding *subintegra* workers and the brood which they carry. This has not been observed by me, although it may occur.

While some of the raids were in progress, a Nemesis in the form of a flicker, *Colaptes auratus* Linn., stood by the side of the trail and picked up some of the *subintegra* workers as they passed in procession. No other predators for either species were observed except a gamasid mite which was found quite commonly on the larvæ, pupæ and callows of the slave species.

The colony of *subintegra* mentioned in this discussion occupied the same nesting site for at least three years and very probably longer. A change in the nesting site of these ants is undoubtedly initiated by a lack of *subsericea* nests for them to raid.

Formica sanguinea subsp. *rubicunda* Emery

This ant, although a close relative of *F. subintegra* and very similar to it in general appearance, can easily be recognized in

the worker caste by the distinctly black-colored gaster and by the broad petiole with sharp superior margin.

F. rubicunda is by no means as common an ant as the foregoing species, being found more sporadically in the area from Canada to North Carolina and westward to Colorado. Wheeler (1913) states that its slaves are other *Formica* belonging to the following species: *F. fusca* var. *subsericea* Say, *cinerea* var. *neocinerea* Wheeler, *neogagates* Emery, *pallide fulva schaufussi* Mayr and its variety *incerta* Emery.

I encountered only three nests of this species at Urbana. One of these, which the ants occupied jointly with their slaves, *F. neogagates* Emery, was a very inconspicuous nest in a garden. As a raid was not in progress at this time no notes were made concerning the ants or their nests.

The second nest was discovered on July 18 at 5.10 in the afternoon, at which time the ants were raiding the nest of a species of *Aphænogaster fulva* var. about eighteen feet from their nest. The *rubicunda* workers after having left their nest crossed a lawn, a graveled driveway, and a portion of the lawn on the adjoining lot. Here they were found taking brood from the nest of the *Aphænogaster* which occurred in the soil beneath some shrubbery. The majority of the *Aphænogaster* workers had been driven from their nest, but a few found in the vicinity of it were trying their best to repulse the attacks of the bold and robust *rubicunda* workers. The sight was somewhat amusing, as the *Aphænogaster* workers appeared very slender and delicate beside their antagonists, for whom it was clearly seen they were no match. I picked up several of the *rubicunda* workers, which bit my fingers savagely, squirting formic acid into the impressions made by their mandibles.

The nest of the *rubicunda* was found to be a small earthen mound about five or six inches high and two to three feet in diameter, which stood out rather conspicuously on the grassy lawn where it was located.

July 15 another *rubicunda* nest was observed which might have been overlooked had I not seen the workers trailing back to their nest with the stolen brood of the slave-species in their mouths. This nest was well concealed beneath a clump of grass

in a lawn. At 1.05 o'clock in the afternoon, the workers were busily engaged in raiding the nest of the ant, *Formica pallide fulva nitidiventris* var. *fuscata* Emery, which was located in the soil near the base of an old stump and about twenty-four paces from the *rubicunda* nest. The bewildered *fuscata* workers were seen running around in the grass in front of their nest, and offering not the least resistance to the *rubicunda* workers, who were securing an extremely large amount of brood. While the raid was in progress other *rubicunda* workers were noted returning to their colony with pupæ and callows of a species of *Formica fusca* (probably *subsericea* Say), which they had obtained from a nest to the west of their own.

Of at least twenty or more raids which I have seen conducted by *Formica rubicunda* and *Formica subintegra*, this is the first time that I have ever witnessed two forays proceeding from the same colony, and at the same time, on two entirely different species of ants. Wheeler (1910) states that colonies of the slave-making species are sometimes found to contain two different species of slaves, but he does not record having seen a raid like the one just described.

Polyergus rufescens subsp. *breviceps* Emery

The so-called occidental Amazon is one of the prettiest and most graceful-looking ants to be found in the vicinity of Urbana. The workers are light yellowish-red in color, with highly polished bodies which glisten in the sunlight in such a manner that the ants are a very beautiful spectacle when on a raid.

This ant has been found to range from California eastward to Illinois and southward to New Mexico. Although it is not a rare ant at Urbana, it is by no means a common species. During my residence there I encountered only two nests of this ant, and had a friend give me specimens from a third nest within the city limits.

Wheeler (1913) states that its slaves are the following species of *Formica*: *fuscata* var. *argentea* Wheeler, *fuscata* var. *subsericea* Say, *cinerea* var. *nocinerea* Wheeler. At Urbana, *subsericea* seems to be the common slave, probably because it is one of our most abundant species of *Formica*. *F. argentea*, although occur-

ring here also, is by no means as common an ant as *subsericea*.

At 4.10 on the afternoon of June 27, 1925, I located a raid of this species which was being carried out on the black lawn ant, *F. fusca* var. *subsericea* Say. The beautiful slave-makers were first observed as they emerged from the obscure nest of the slave-species located in the grass near the edge of the sidewalk. Nearly every *breviceps* worker bore a pupa of the slave-species, which it was carrying with alacrity to its nest. The raid must have been under way for some time, for the *subsericea* workers had fled from their nest and left their brood exposed to the mercy of the marauders. The *breviceps* workers were returning to their nest in a file, which at some places was only one worker broad and at other places ten to twelve workers broad. This trail led across a street, in which many automobiles were passing to and fro and undoubtedly killing many of the ants, yet the raid continued in spite of such disturbances. I trailed the ants back to their nest which was found on the east side of a house, in the soil just beneath the ledge of a basement window. This nest was at least seventy-five yards from that of the *subsericea* colony, which it was raiding.

On questioning the owner of the house as to the length of time that the ants had been under his observation, he stated that he had observed the colony of *Polyergus* when he moved into the house five years previously and that he believed the ants had been there for sometime before he moved in.

On July 16, 1926, a raid by this species was observed between 4.30 P. M. and 5.05 P. M. This raid by a second colony of *breviceps* was on another nest of the same slave-species. The nest of the slave-species was found to be sixty paces to the south of that of the *breviceps*. The raid resulted as usual in the slave-makers securing a large amount of brood with but little opposition from the slave-species.

At 5.05 P. M., July 21, 1926, I went to the nest of the colony of *breviceps* mentioned above to see what was taking place. This nest was located in the soil beneath the ledge of a basement window, on the west side of the old Agricultural Building of the University of Illinois. At this time, only a few stray workers of *breviceps* could be seen above the surface of the ground.

Hoping to locate some of the ants, I began to remove some of the dirt from around their nest. Almost immediately the yellowish-red workers began pouring forth, appearing to be in much of a rage. Some of them settled on the handle of a trowel that was lying on the ground, and so firmly did they fasten their mandibles into the wood, that when I gave the trowel a very sharp shake, I could not dislodge the ants. For a few minutes the ants ran around on the ground in a more or less aimless way although a few of the workers would occasionally stop and touch each other with their antennæ, whereas others rubbed the sides of their bodies against the ground in such a manner that it gave me the impression they must be stridulating. At any rate, it was only a short time until the ants set out in a concerted mass for a *subsericea* nest which lay ninety-five paces distant. In going to this, the ants had to cross a large amount of thick grass, a cement walk and some tilled soil. While on the march they kept in a rather compact file about twenty feet long and not over four inches wide. After a comparatively short time they succeeded in reaching the *subsericea* nest. When a sufficient number were present, they poured into the nest of the slave species and in a few seconds were victoriously emerging with larvæ and pupæ of the latter. Most of the *subsericea* had fled from their nest on the approach of the *breviceps* workers, and those which were left were immediately pounced upon and dispatched by the slave-makers. The *breviceps* workers set off for their nest in a very brisk and decided manner, covering the entire distance of about 237.5 feet in thirty-eight minutes, or at an average speed of about 6.5 feet per minute. Wheeler (1916) found that the workers of this species could travel 5 feet per minute over the mountainous soil in California. The speed at which the ants travel and also the deliberateness of their manner is most striking when *breviceps* is compared with the species of *sanguinea* discussed above. Hastening to the *breviceps* nest to examine it before the slave-makers returned, I found there only a very few *breviceps* workers but many workers of the slave-species.

As mentioned above, *Polyergus breviceps* differs from the species of *sanguinea* in several respects. Raids by this species are apparently never made in the forenoon, at least they have

never been observed. It is believed that the raids are initiated by certain temperature requirements which do not reach an optimum until the afternoon. Another peculiarity of these ants is that the alate or déalate females may join in the raids which the workers are making on the slave-species. No one, however, has even seen the females return to their nest with brood appropriated from the nest of the slave-species. In California, Wheeler watched the females leave on the raids, but he did not see them return to their nest. One is naturally led to wonder if these females secure immediate adoption in the nest of the disconcerted slaves and fail to return to their own nest, or do they join the raid in order to locate the nests in which they hope to secure adoption later?

The founding of colonies by the females of the species of *Polyergus* and those of *sanguinea* does not differ much in detail. Wheeler has shown that a fertile female of either form seeks out a nest of the slave-species and attempts to secure adoption in the nest. In the case of the *sanguineas* the female attempts to appropriate the brood of the slave-species, and when the slave-workers attempt to rescue the brood from her the female kills the workers. It is not clear whether she slays the female of the slave-species also, or whether this female is later slain by her workers, as is the case with some of the other species of ants. Whatever may be the method employed, the *sanguinea* female, if successful, rears the slave brood to maturity, and these alien workers in turn rear her young, so that in the course of time the colony becomes a mixed one. When the colony is of sufficient size, the *sanguinea* workers then begin to seek out nests of the slave-species and to raid them, appropriating the brood of the slaves as their mother before them has done. The *sanguinea* workers, although able to make slaves, have by no means lost their power to rear young or to construct nests when the necessity arises; hence the species cannot be considered obligatory slave-makers as are the species of *Polyergus*. The latter are not only dependent on their slaves for food, but also for the care of their young and the construction of their nest. The female of *breviceps* when she enters a slave nest secures adoption only after she has slain the female of that colony. That the workers of

breviceps or either of the two species of *sanguinea* mentioned here should seek to appropriate brood of certain slave-species is not surprising, when we consider that they are only acting in the same manner as their mother before them did. The habits of the slave-making species are very similar to those of the temporary parasitic ants, the only difference between the two being that the temporary parasitic ants never make dulotic raids on their host species.

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